

VIII. *On the Frenulum of the Lepidoptera.* By  
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PLATE IV.

THE existence of an apparatus for connecting the fore- and hindwings of many of the Lepidoptera was first noticed by the Swedish naturalist, De Geer, in the first volume of his "*Mémoires pour servir à l'Histoire des Insectes*," published in 1752. He there describes "a process curved like a hook, situated on the under surface of the forewing near its base, which holds with its point a long stiff hair springing from the basal portion of the hindwing." This, he says, he has found in the males of all species of nocturnal Lepidoptera in which he has sought it, but not in any of the Diurni. He failed, however, to detect the corresponding appliance in the females, and in summing up his account of the organ candidly owns himself to be ignorant of its use, though he seems to have recognised that it has the effect of making the fore- and hindwings act in unison.

The next mention of the appliance occurs in an essay on the "Tendons and Membranes of the Wings of Butterflies" by Moses Harris, 1767. The author figures and describes the spring or bristle and observes that it pertains only to the males, the females having instead of the spring four small hairs or bristles.

On the 2nd June, 1789, a paper entitled an "Account of a singular conformation in the wings of some species of moths," by Esprit Giorna of Turin, was read before the Linnean Society and published in its Transactions, i, p. 135.

The author was unaware of De Geer's previous reference to the subject, and lays claim to the discovery of the appliance. To this he is, in fact, partially entitled, as he supplements the research of the earlier observers by calling attention to the corresponding apparatus to be found in the females of many species. He gives a list of some

seventy species examined, and his remarks as to these are for the most part correct and show careful observation, though in one or two instances in which the organ is weakly developed it appears to have been overlooked by him.

Kirby and Spence refer somewhat at length to the appliance but state that it is found "in many male butterflies, hawk-moths and moths." Later observers, however, have determined that, as regards the *Diurni*, it occurs only in one or two species of the *Hesperiidæ*, which in some other respects partake of the characters of the *Heterocera*. Blanchard, indeed, has given the name *Achalinoptera* to the butterflies and *Chalinoptera* to the moths on account of the absence or presence of the apparatus, but this, as will presently be seen, is not of sufficiently general occurrence to be made use of as a discriminating character of such importance. Kirby and Spence refer rather unfortunately to the organ of the male as consisting of one *or more* bristles but add that the females often have the bristles, but never the hook.

Burmeister in his "*Handbuch der Entomologie*," and Boisduval in the "*Spécies général des Lépidoptères*," 1836, both refer at some length to the frenulum, as also does Prof. Westwood in his "*Introduction to the Modern Classification of Insects*," 1838.

Dr. Chenu in his "*Encyclopédie d'Histoire Naturelle*" (Vol: *Papillons Nocturnes*, by E. Desmarest) mentions the organ, but assigns as its object the maintenance of the wings in a horizontal or an inclined position during *repose*.

It will be evident from the above that the accounts of the frenulum as given by various authors differ both as to its development and its purpose.

In commencing an examination of the subject several years ago this was brought strongly under the notice of the writer at the outset, and it seemed that much might still be learned from a study of the appliance in a large number of examples extending over the various groups and genera of the *Heterocera*. Accordingly an examination, either microscopic or by means of a platyscopic lens, has been made of the majority of our British moths, including the so-called *Micro-lepidoptera*, and of several hundred species of exotic *Heterocera*. The results of this investigation are here recorded.

Since this examination has been in progress Prof. Comstock in his essay, "Evolution and Taxonomy," published in 1893, and subsequently in his "Manual for the Study of Insects," 1895, has formulated a classification of the Lepidoptera principally based on wing-characters. He proposes a division of the Order into two Suborders, Frenatæ and Jugatæ, the former of which embraces all those species which either possess this structure or appear to be descended from groups formerly possessing it, whilst the Jugatæ have the wings united by a lobe or jugum. The latter Suborder consists only of the Hepialidæ and Micropterygidæ, which are certainly some of the most primitive of the Lepidoptera, and in other respects, as well as in the possession of the jugum, are clearly related to the Trichoptera.

With the merits of this classification we cannot deal, but will simply observe that the frenulum is scarcely so persistent or general in its occurrence as to give its name to a broad division of the Lepidoptera.

Mons. E. L. Ragonot (*Essai sur la Classification des Pyralites*, 1891), Sir George F. Hampson (*Fauna of British India—Moths*, 1892-96), Mr. E. Meyrick (*Handbook of British Lepidoptera*, 1895), and Dr. A. S. Packard (*Monograph of the Bombycine Moths of America North of Mexico*, 1895) have all considered the frenulum with great care, employing it with other characters in discrimination of genera, whilst they do not attribute to it the supreme importance claimed by Comstock.

Speaking generally, and with certain exceptions to be mentioned later, we find in those species which possess the frenulum that the males have a strong single bristle, springing from the costal nervure of the hindwing, and passing through a loop, or sometimes into a pocket, situated on the costal nervure of the forewing; that the females usually possess two or more slender and weak bristles upon the hindwings in place of the single bristle of the male insect, and that these bristles, instead of passing into a loop, are simply thrust into, and entangled among, a group of large raised scales or hairs situated between the costal and median nervures of the forewings.

And here at the outset we meet with a difficulty arising from the confusion of names applied by different authors to the various parts of this appliance. Whilst De Geer speaks of the bristle under the name of *poil* and

denominates the loop *crochet*, Giorna calls the former *ressort*, *appui* or *fulcrum*, and the latter *anneau*. Kirby and Spence name the bristle *tendo* and the loop *hamus*; Boisduval appropriates to the bristle the names of *erin* or *frcin* and to the loop that of *coulisse*; some authors following him so far as the bristle is concerned give it the Latinised designation of *frenulum*, whilst Burmeister speaks of it as *erin* or *subula*, at the same time applying to the loop the name of *frenulum*.

In view of the confusion arising from these various names it seems convenient in this paper to retain the name *frenulum* for the organ as a whole; to speak of the strong single bristle of the male insect as the *spina*, referring to the group of smaller bristles of the female under the diminutive plural *spinulæ*; to speak of the loop which holds the bristle of the male as a *retinaculum*, the term now in general use by Hampson and other recent writers, and to refer to the bunch of scales in the female as a *fasciculus*.

Having thus cleared the ground, we may now consider the varied development of this organ as observed in the several divisions of the Lepidoptera.

The only Rhopalocerous insect known to the writer as having the frenulum completely and functionally developed, is the very curious and interesting Hesperiid from Queensland, *Euschemon rafflesia*.

In the male (Fig. 14) the spina is strong and of considerable length and works through a fully developed retinaculum, bare or almost bare of scales. In the female the spinulæ are perceptible only with difficulty, and are short and weak bristles, five in number, probably of little or no value to the insect. In the "Classification of the Hesperiidæ" by Lieut. E. Y. Watson (P.Z.S. 1893, p. 3) this insect is omitted from the list and is considered to be a moth, principally on the ground that it possesses the frenulum; but at that time the larval and pupal stages were unknown. The writer is glad to be able to announce that these have now been discovered by a correspondent in Queensland, and as in both stages the insect is clearly allied to the Hesperiidæ, its claim to be placed among them will probably be fully sustained. Two or three other exotic species of Hesperiidæ possess small bunches of hair-like scales upon the hindwings which are evidently rudimentary spinæ, but these are unaccompanied by even

a trace of the retinaculum and are quite useless: they are, however, very interesting as showing the near relationship of these insects to the Heterocerous Lepidoptera.

The Sphingidæ exhibit the highest development of the frenulum, the spina of the male insect attaining its maximum of size and strength and the retinaculum being powerful and capable of holding with a firm grip. In the female insect too the spinulæ are strong, and their extremities converge to a strong fine point, thus forming a claw or hook, which catches the fasciculus of the forewing with considerable effect. These characters hold good as regards the majority of the species of this family, but some members of the subfamily Smerinthinæ form a noteworthy exception. Of one of these, *Smerinthus populi*, Giorna states in the paper referred to, that it is without the appliance. Such, however, can hardly be said to be the case; the male insect possesses, in the position occupied by the spina in other species, a process standing out from the margin of the wing, rounded in outline and in some few examples terminated by a minute point (Fig. 4). This process corresponds to the root or prominence which in other species carries the spina.

The female has a much more largely developed apparatus; not only does she possess the root-process, but also a perfectly formed group of spinulæ (Fig. 5), which, however, are too small to be of any practical use in connecting the wings; so that the organ in both sexes may be considered abortive.

The retinaculum of the male is absent, as we might expect, and its place is simply indicated by a most inconspicuous group of scales. It will be evident on consideration that the peculiar rest-position always assumed by *S. populi* would be quite impossible in a species with fully developed spina and retinaculum, inasmuch as the humeral angle of the hindwing always projects before the costal margin of the forewing, and it would be necessary for the moth to withdraw the bristle from its loop every time that it composed its wings for rest.

A similar rudimentary development of the part also occurs in greater or less degree in several other allied species, notably in the fine Australian species, *Cæquosa triangularis*, which has the spina very short and probably quite useless. Some other Smerinthinæ, however, such

as the genus *Mimas* of Hübner, which includes *M. tilia* and *M. quercus*, have the appliance fairly well developed. So also the very fine and remarkable South African moth, *Lophostethus dumolini*, which is usually referred to the Smerinthinæ, has the organ well and strongly developed in both sexes.

The flight of many Smerinthinæ is so different from that of the typical Sphingidæ, and their habits are so much more sluggish, that it is interesting and instructive to find a diversity in the perfection of this apparatus.

Further, as we shall presently see, the spina and retinaculum are absent in the Saturnias and Attaci, thus affording another character which strongly supports Prof. Poulton's contention (Trans. Ent. Soc. Lond., 1888, p. 568) that the Smerinthi are closely connected with the Attaci in their natural affinities.

In the Zygaenidæ the retinaculum, instead of being hook-like or ring-like, resembles a long pocket upon the costal nervure into which the spina fits somewhat closely, the point being sometimes just visible at the extremity, but often quite concealed (Fig. 10). The genus *Himantopterus* belonging to this group is however without the frenulum (Hampson—Moths of India, i, p. 288).

The Cossidæ have the frenulum present but it is absent in the Arbelidæ.

The Lithosiidæ are possessed of the frenulum but in certain genera, *Padenia*, *Garudinia* and *Pseudoblacus* the costa of the forewing has a strong fold, holding that of the hindwing; this fold is more largely developed in the male than in the female (Hampson, *l. c.* ii, pp. 97, 98).

Both the Agaristidæ and the Arctiidæ have the process strongly and fully developed, the retinaculum in many of the latter being of very unusual length (Fig. 8).

The Lymantriidæ also possess the frenulum, with the exception of the genus *Ratarda* in which it is absent (Hampson, *l. c.* i, p. 493).

In the Callidulidæ one genus, *Cleosiris*, is quite without the frenulum, whilst in another genus, *Herimba*, the spina is long, the retinaculum of the male arising from the sub-costal nervure of the forewing. In the other genera of this family, *Callidula* and *Pterodecta*, the frenulum is present but minute; the retinaculum arises from below the median nervure (Hampson, *l. c.* i, p. 322).

In the Bombycidæ, Saturniidæ and Lasiocampidæ a



large number of species have been examined, and in all of these the frenulum is found to be entirely wanting. The rudiment of the spina may indeed be detected, as is observed by Burmeister. It is enclosed in the membrane of the hindwing, but is perfectly useless, and does not even extend to the edge of the wing. When we consider the shape of the wings in this group we perceive that the frenulum is not required, as the anterior angle of the hindwing is carried forward in a kind of shoulder almost or quite to the costal nervure of the forewing, and as this nervure in many species bends back over the surface of the wing, it seems probable that during flight the prominent shoulder of the hindwing locks beneath it. The common silk-worm moth, *Bombyx mori*, however, which has this configuration of wing, still possesses a very small rudimentary spina, as do also the two remarkable North-American moths, *Cicinnus melsheimerii* and *Lacosoma chiridota* referred to by Comstock (Study of Insects, p. 357).

The Uraniidæ, so difficult to assign to a satisfactory position in classification, exhibit a similar development of the humeral portion of the hindwings, and both spina and retinaculum are absent so far as the genus *Urania* is concerned. *Nyctalemon* has in some few instances a very imperfect rudiment, but *Sematura* possesses the appliance, although so feebly developed as to be of very little use. *Coronis*, on the other hand, in the thirteen species which have come under the writer's observation, has a frenulum, the bristles of which, although rather slender in both sexes, are in all cases sufficiently strong to be effective.

In the Epicopiidæ the spina is quite rudimentary. The late Mr. G. R. Gray in his classification of the difficult group Castniidæ (Trans. Ent. Soc. Lond., ii) based his division in part upon the development of this organ, assigning to some species the possession of three, and to others of four, "wing-guides." Unfortunately the specimens, upon which these characters were founded, must have been females, as examination shows that this singular group is in accord with nearly all others in which the frenulum is found, in having the spina single in the male and double at least in the female.

The Notodontidæ possess the frenulum, but in many species in little more than a rudimentary degree, that of *Stauropus fagi* in particular being very small.

Amongst the Drepanulidæ the humeral angle of the

hindwings is largely developed, but all our British Hook-tips have a weak and slender frenulum in the male, and a small bunch of spinulæ in the female, which is probably of little or no functional value. The organ is absent altogether, according to Hampson and Comstock, in the genera *Phalaera* and *Orecta*.

Nearly all the species of the great family Noctuidæ possess the frenulum in normal development, though slight variations in the strength of the bristles occur in certain genera. Of the genus *Stictoptera*, however, which has not come under the writer's observation, Hampson remarks:—"Frenulum of male very strong; single in female." This single spina of the female is very interesting, as being at variance with all the nearly related genera.

In the Geometridæ the frenulum is found in the great majority of the genera, but, as may be expected from the frail and slender structure of their wings and bodies, it is of weaker development than in the stronger-bodied Noctuidæ. In the genera *Pseudoterpna*, *Geometra* and *Phorodesma*, however, the humeral angle of whose hindwings is much extended, we find in the male the spina very weak, and in the female the spinulæ either nearly rudimentary or altogether wanting, whilst in *Iodis* the frenulum is entirely absent in both sexes. In one section of *Synechia*, as defined by Hampson (*Moths of India*, iii, p. 167) the retinaculum is a tuft of hair, in a second it forms a large spatulate plate, whilst in a third it is described as bar-shaped. Other genera according to the same author lack the organ, namely, *Genusia*, *Hypulia*, part of *Naxa*, *Eucrostes*, *Paramaxates* and *Thalera*.

Writing of the Sesiidæ, Prof. Comstock (*Study of Insects*, p. 260) says:—"Another remarkable feature of all the forms that we have studied is that in the female the bristles composing the frenulum are consolidated as in the male." Amongst our British Sesiæ this holds good in respect of *Sesia ichneumoniformis* and *S. cynipiformis*; but *S. myopæformis* ♀ and *S. tipuliformis* ♀ (Fig. 15) have the spina single for about one-third of its length and bifid at the tip. As *S. tipuliformis* occurs in North America, this peculiarity has apparently been overlooked by Comstock; this is not surprising, as the spina under microscopic examination appears at first sight to be single, and its divided nature is only revealed when subjected



to slight pressure. The spina of the female rests under a catch composed of scales proceeding from the costal nervure of the forewing, which bends over very strongly. It is to this catch that Prof. Comstock probably refers when he goes on to remark:—"The females also possess a frenulum-hook; but this is not so highly specialised as that of the male." It may be mentioned that *Sesia omphale*, ♀, a native of Florida, has a weak double spina, and that *Trochilium crabroniforme*, ♀, has a frenulum composed of five spinulæ locking into scales upon the median nervure, as in the normal development of this appliance.

The Tortricina and the majority of the Pyralidina have the frenulum of the usual character, but it is in some of the members of the latter group that the most singular variations of this organ exist. Hitherto we have found that the spina of the male insect works through a retinaculum arising from the costal nervure of the forewing: but in several species of our British Pyralides the male spina locks into a fasciculus of strong scales on the median nervure of the wing, in fact in the manner generally characteristic of the organ in the female. Amongst these species are *Agrotera nemoralis*, *Endotricha flammealis*, *Diasemia literalis*, *Stenia punctalis*, *Botys flavalis*, *B. fuscalis*, *B. verticalis* and *B. asinalis*. In each of these species the female insect has two spinulæ, but in *Cataglyphis lemnales* (Fig. 16) which has the male frenulum as above described, the female has a single spina exactly similar to that of the male. In the subfamily Phycitinae according to Ragonot (Mon. Phyc. 1894) and Hampson (Moths of India, iv, p. 64) the spina of the frenulum is simple in the female, as in the male. A striking peculiarity of the Chrysauginæ is referred to by Ragonot (Essai sur la Classn. des Pyralites, 1891) and Hampson (P.Z.S. 1897, p. 633). In many species the spina of the male is described as being much thickened, flattened and contorted, and in some instances accompanied by a strong lower fork; this very singular development does not appear to have its parallel in any other group.

Certain species of the genus *Crocidolomia* referred to by Hampson (Moths of India, iv, p. 371) have a thick tuft of hair springing from the subcostal nervure, whilst from a fringe below the median nervure arise four strong curved spines playing on the subcostal tuft. At first sight these

processes appear to be ancillary to the frenulum, but a careful examination by the writer of several specimens from Queensland, leads to the conclusion that this is not the case. No binding of the wings can be due to these spines, as both they and the tuft of hair belong to the forewing only, whilst the supposition that they hold down the point of the spina after passing through the retinaculum is negatived by the fact that they are at too great a distance from the base of the wing to come in contact with it.

The great division of the Tineina, which has been observed by several recent writers to be of a very heterogeneous character, proves to be so also in respect to the frenulum. Whilst the great majority of the species possess it and in numerous instances the spina is of a greater size in proportion to that of the insect than in many of the larger moths, yet in one or two groups it is found to be wanting. In the Nepticulidæ, particularly, this is the case; also in *Micropteryx*, which in most of its species has a well-developed jugum, this is only rudimentary however in *M. calthella* and *M. scypella*. Several species of this group have a few strong hairs on the costal margin of the hindwing, which, as Dr. Chapman points out, may be a commencing frenulum.

Turning next to the structure of the organ under consideration we find on microscopic examination that the spina of the male insect, simple and homogeneous as it appears at first sight, is really composite in its character. Viewed under a high power its apparently polished and smooth surface is seen to be deeply furrowed with fine longitudinal lines, and the significance of this is made clear when, on making a transverse section, we find that the spina is really an agglutination of tapering hollow tubes or hairs, and is in fact evolved from the less perfect organ of the females by fusion of the bunch of spinulæ into one strong bristle. Being thus made up of hollow tubes the spina possesses great elasticity as well as strength.

The spinulæ of the female when microscopically examined are found to be simple hollow tubes, and these, with the few exceptions just cited, vary in number from two in some species, to upwards of twenty in others. They spring like the spina of the male from a raised socket formed by an extension of the costal nervure of the hindwing.

The retinaculum in its normal form is a process springing out of the substance of the costal nervure of the forewings, and curling over at the end into a small loop or ring; this process is usually thickly covered with scales. In those cases before-mentioned in which its form is that of a pocket receiving the point of the spina, rather than a loop, this pocket is formed in the same way from the substance of the nervure, and in most cases it also is clothed with scales.

The fasciculi or bunches of scales which receive and hold the spinulæ of the female are larger and longer than the other scales of the wing, but beyond this they possess no distinguishing character. Whilst speaking of these we must not forget to notice certain long bunches of hair-like scales which are often found associated with this organ; these proceed from the thorax of the insect and lie across the spina or spinulæ, thus probably helping to keep them in position.

We have next to consider the two different purposes assigned to this appliance by various observers, namely, the holding of the wings in position during repose, or, as an alternative, the locking together of the fore- and hindwings as an aid in flight. With a view to ascertain the correctness or otherwise of the first supposition, the spinæ of several living male specimens of moths were amputated, such species being selected as assume a well-marked and striking position during repose—*Pygæra bucephala* and *Sphinx ligustri* being amongst those experimented upon. In every case the original rest position was again assumed by the insect after the operation.

The behaviour of these insects, having one or both of the spinæ removed, was then observed during flight, the movement of their wings being watched as they flew up and down before the glass of a closed window. In all cases in which one spina only was amputated, a difference in the blur of the rapidly moving wings was noticed, the wings on the side experimented upon being observed to move more independently of each other. These experiments being conducted within-doors in order to prevent the escape of the insect, the conditions were somewhat unnatural, and no very clear idea could be arrived at respecting the actual loss of power of flight resulting from the want of one or both spinæ. It is probable that the effect of the wind upon a moth so situated would be very

great, for the wings which before presented one broad strong surface to the breeze, would after the amputation of the spina lose much power by the escape of the air between them, and would probably be bent or displaced if the wind were at all boisterous.

Another point having a bearing upon the question of the use of this apparatus was noticed in a female specimen of *Deilephila euphorbiæ*, and might no doubt be observed in many other species. The insect resting on a flat surface with its wings outspread held the anterior margin of the hindwings in such a position as to be just in contact with the costal nervure of the forewings, but on being disturbed it prepared for flight by bringing forward the front pair slightly, and strongly depressing their points. This clearly forces the spinulæ into close contact with the fasciculus of long scales destined to receive and hold them, and thus locks the wings firmly together. This proceeding was gone through by the insect again and again on being disturbed, and is evidently its first preparation for flight.

In the examination of living specimens the writer was at first somewhat doubtful whether the male insect, if by accident it should withdraw its spina entirely from the retinaculum, would be able to replace it at will, but this point was cleared up by the chance discovery of a male specimen of *Ennomos angularia* lying upon its back in a pool of water. On examination the spina of the left wing was found to be withdrawn from its retinaculum. It was placed in a position in which it could dry its wings and from time to time examined to ascertain whether the spina had been replaced. Before the next morning the moth had once more inserted it in the retinaculum.

It seems clear from the foregoing experiments that the purpose of the frenulum is to hold the wings together during flight, and this conclusion is accepted by most recent writers. The organ is therefore analogous in its purpose to the less perfect jugum of the Trichoptera and *Micropteryx*, to the wing-hooks of the Hymenoptera and to the locking apparatus of *Belostoma*.

#### PLATE IV.

[The explanation faces the PLATE.]